

Range extension and new records of Tailed Tailless Bat, *Anoura caudifer* (É. Geoffroy, 1818), in northeastern Brazil

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Abstract. We report on the occurrence of *Anoura caudifer* (É. Geoffroy, 1818) in northeastern Brazil and expand its known geographic distribution. The new records are from the Ceará and Bahia states. The record from Ceará is the first from that state, and the two new records from Bahia are from the northern part of that state. These records extend the known distribution of *A. caudifer* by 600 km in the eastern South America.

Key words. Caatinga, Chiroptera, Glossophaginae, morphology variation, nectar-feeding

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INTRODUCTION

Bats of genus *Anoura* Gray 1838 (Chiroptera, Phyllostomidae) are small, nectar-feeding bats that pollinate several species of flowering plants and have importance in ecosystem services (Fleming and Sosa 1994; Kunz et al. 2011). The genus currently contains 10 species that may be artificially divided in two taxonomic complexes: the “large *Anoura*, *geoffroyi* complex”, which includes *A. geoffroyi* Gray, 1838, *A. peruana* Tschudi, 1844, *A. cultrata* Handley, 1960, and *A. latidens* Handley, 1984, and the “small *Anoura caudifer* complex”, including *A. caudifer* (É. Geoffroy, 1818), *A. aequatoris* (Lönberg, 1921), *A. luismanueli* Molinari, 1994, *A. fistulata* Muchhala et al., 2005, *A. cadenai* Mantilla-Meluk & Baker 2010, and *A. javieri* Pacheco et al., 2018 (Pacheco et al. 2018; Cirranello and Simmons 2020; Calderón-Acevedo et al. 2022; Molinari et al. 2023). *Anoura* species may be easily identified by the little-developed uropatagium, the presence of three upper molars, the absence of lower incisors, and by their inner incisors which are smaller than their outer incisors (Saussure 1860; Miller 1907).

Anoura species occur in most of the South American continent except in the Chilean territory (Griffiths and Gardner 2008). Many *Anoura* species occur in the Andes cordillera (Molinari 1994; Muchhala et al. 2005; Mantilla-Meluk and Baker 2006, 2010; Pacheco et al. 2018; Molinari et al. 2023). On the other hand, eastern South America apparently has a less diverse *Anoura* fauna, including the more broadly distributed *A. caudifer* and *A. geoffroyi*. Of these, the smaller *A. caudifer* has been recorded from Paraguay and northern Argentina north to Bolivia, Peru, Colombia, Ecuador, Guyana, Suriname, French Guiana, Venezuela, and a large part of Brazil (Oprea et al. 2009). *Anoura caudifer* has thought to be associated with tropical forest environments, and records from drier regions have been neglected in recent compilations (Griffiths and Gardner 2008; Oprea et al. 2009; Solari et al. 2020).

Within Brazil, *A. caudifer* has been recorded in forests and cangas in the Amazonian biome in the states of Acre, Amazonas, Amapá, and Pará (Peracchi et al. 1984; Reis and Peracchi 1987; Santos and Gibson 1998; Nogueira et al. 1999; Martins et al. 2006, 2011; Tavares et al. 2008, 2012; Hoppe and Ditchfield 2016; Alves et al. 2021; Mourão et al. 2022), Atlantic Forest (Marinho-Filho and Sazima 1989; Teixeira and Peracchi 1996;



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Trajano 1996; Reis et al. 2000; Esbérard 2003; Sá-Neto 2003; De Knecht et al. 2005; Vaz 2005; Barros et al. 2006; Faria et al. 2006; Moratelli and Peracchi 2007; Modesto et al. 2008; Tavares et al. 2008; Nascimento et al. 2010; Velazco et al. 2010; Chaves et al. 2012; Gruener et al. 2013; Albuquerque et al. 2013; Carvalho et al. 2013; Teixeira et al. 2013; Muylaert et al. 2014; Lapenta and Bueno 2015; Lima et al. 2016; Pedrozo et al. 2016; Rocha and Bichuetti 2016; Dornelles et al. 2017; Costa et al. 2018; Carvalho et al. 2020; Cláudio et al. 2020; Hoppe et al. 2020), Pantanal (Mourão et al. 2002; Cáceres et al. 2007; Cunha et al. 2011; Eriksson et al. 2011; Oliveira et al. 2012; Barbier and Gracioli 2016), and Cerrado (Bredt et al. 1999; Rodrigues et al. 2002; Gonçalves and Gregorin 2004; Bordignon 2006; Urbietta et al. 2014; Fischer et al. 2015; Lapenta and Bueno 2015; Felix et al. 2016; Lima et al. 2017; Pereira et al. 2018).

Anoura caudifer may be distinguished from its congeners in Brazil by its wide, sparsely haired interfemoral membrane, which is semicircular in shape. In contrast, *A. geoffroyi*, which is slightly larger than *A. caudifer* (i.e. forearm >40 mm and greatest length of skull >24 mm) has a densely haired interfemoral membrane, which is triangular and reduced to a narrow band (Griffiths and Gardner 2008; Mantilla-Meluk and Baker 2010).

Here we report the northernmost locality in the northeastern South America of *A. caudifer* in the Caatinga biome, in Ceará state, Brazil (Figure 1). We provide a revised distribution map for this species, and we also report on the morphological variation in this species.

METHODS

We considered the distribution of *Anoura caudifer* in South America based on the data available in the recent compilations of Solari et al. (2020) and Marsh et al. (2022), and complemented these data with

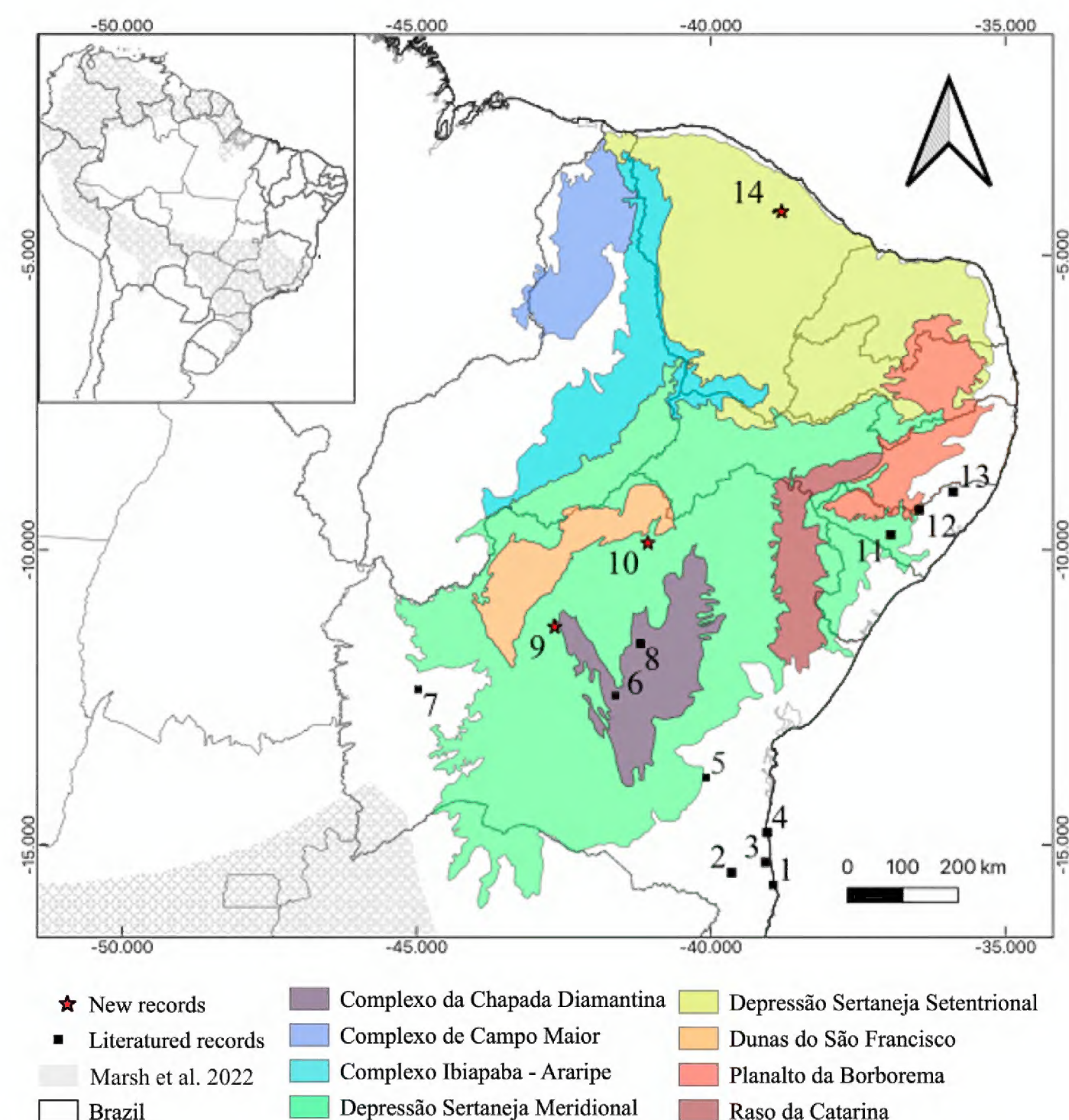


Figure 1. Geographic distribution of *Anoura caudifer* in northeastern Brazil, including previously known and new records. Inset map: global distribution according to the IUCN (grey-shaded area). Literature records: 1 = Canaveiras, 2 = Pau Basil, 3 = Una, 4 = Ilhéus, 5 = Jequié, 6 = Palmeiras, 7 = São Desidério, 8 = Morro do Chapéu, 11 = Traipu, 12 = Quebrangulo, 13 = Ibateguara. New records (★): 9 = Gentio do Ouro, 10 = Piçarrão Sento Sé, 14 = Guaramiranga.

records added from our review of the literature (i.e. records supported by voucher deposited in collections) and by our own observations of specimens from the collections of Universidade Federal da Paraíba (UFPB), João Pessoa, PB; Universidade Federal de Pernambuco (UFPE), Recife, PE; and Museu de História Natural do Ceará Prof. Dias da Rocha (MHNCE), Pacoti, CE. We took external and skull measurements using digital calipers to the nearest 0.01 mm according to Calderón-Acevedo and Muchhala (2018) as follows: forearm length (FA), greatest length of the skull (GLS), palatal length (PAL), condylobasal length (CBL), maxillary tooth-row length (MTRL), breadth across third upper molars (M3–M3), breadth across upper canines (C–C), height of brain case (HBC), postorbital breadth (PB), mastoid breadth (MB), brain case breadth (BCB), mandibular length (MANL), and mandibular tooth-row length (MANTRL). We comparatively studied the museum specimens based on the morphological characters normally used to differentiate *A. caudifer* from other *Anoura* species taking notes and making drawings and sketches with additional observations.

RESULTS

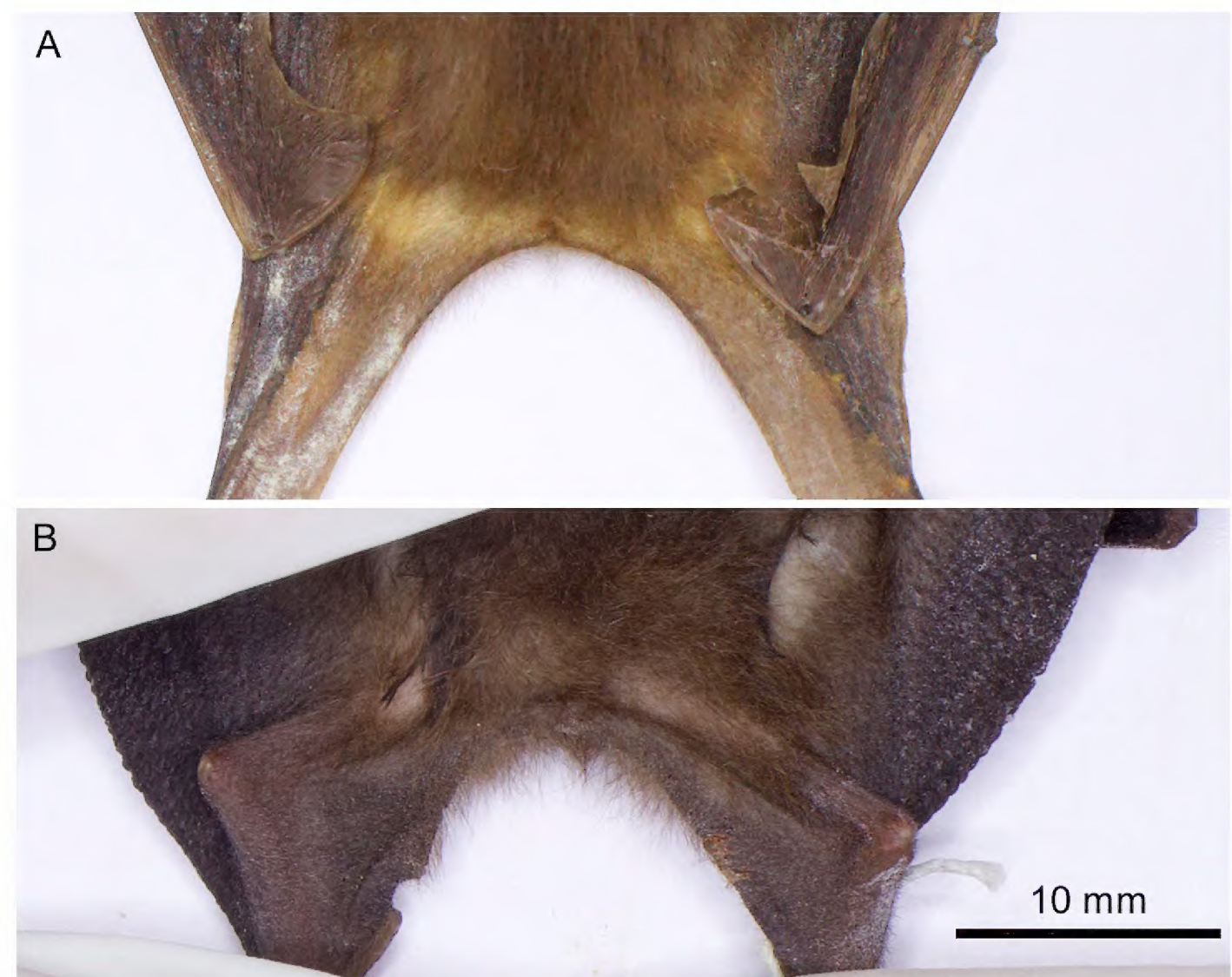
Anoura caudifer (É. Geoffroy, 1818)

Figures 2, 3

New records (Fig. 1). BRAZIL – **Ceará** • Guaramiranga, Reserva Particular do Patrimônio Natural Sítio Lagoa; –04.262, –038.932 (locality 14, Fig. 1 and Fig. 2); alt. 865 m; 29.V.2022; N. Cavalcante leg.; MHNCE 418, 1 adult ♂ – **Bahia** • Gentio do Ouro, Gameleira do Assuruá; –011.301, –042.656 (locality 9, Fig. 1); alt. 404 m; 27.V.2015; A. Feijó leg.; UFPB 11520 & 11521; 2 adult ♀ • Gentio do Ouro, Gameleira do Assuruá; –011.301, –042.656 (locality 9, Fig. 1); alt. 404 m; 27.V.2015; A. Feijó leg.; UFPB 11523; 1 adult ♂ • Piçarrão Sento Sé, Parque Nacional Boqueirão da Onça, –09.745, –041.885 (locality 10, Fig. 1); alt. 416 m; 19.V.2015; A. Feijó leg.; UFPB 11496; 1 adult ♀ • Piçarrão Sento Sé, Parque Nacional Boqueirão da Onça, –09.745, –041.885 (locality 10, Fig. 1); alt. 416 m; 19.V.2015; A. Feijó leg.; UFPB 11500 1 adult ♂ • Piçarrão Sento Sé, Parque Eólico Sete Gameleiras; –09.745, –041.885 (locality 10, Fig. 1); alt. 416 m; 11.III.2012; A. Feijó leg.; UFPB 6491, 6492, 6643, 6668 and 9723; 5 adult ♀ • Piçarrão Sento Sé, Parque Eólico Sete Gameleiras; –09.745, –041.885 (locality 10, Fig. 1); alt. 416 m; 11.III.2012; A. Feijó leg.; UFPB 6651; 1 adult ♂.

Identification. The specimens were identified based on forearm length, tail presence, and skull characters (Fig. 3). *Anoura caudifer* can be distinguished from *A. geoffroyi*, *A. peruana*, *A. cultrata*, and *A. latidens* by its smaller size (forearm length <40 mm; Table 1) (Handley 1960, 1984). In contrast, *A. caudifer* is larger than *A. luismanueli* (forearm <34 mm; Molinari 1994). *Anoura fistulata* can be separated from *A. caudifer* based on lower lip morphology—in *A. fistulata* the lower lip protrudes forward from the upper lip by approximately 3 mm—and based on skull length (24.10 mm ± 1.34 in *A. fistulata*) (Muchhala et al. 2005). While there is a small tail in *A. caudifer*, a tail is absent in *A. cadenai* (Mantilla-Meluk and Baker 2006). *Anoura javieri* is

Figure 2. Dorsal view of the uropatagium of *Anoura caudifer*. **A.** containing scarce fur (UFPE 1342). **B.** densely furred (MHNCE 418).



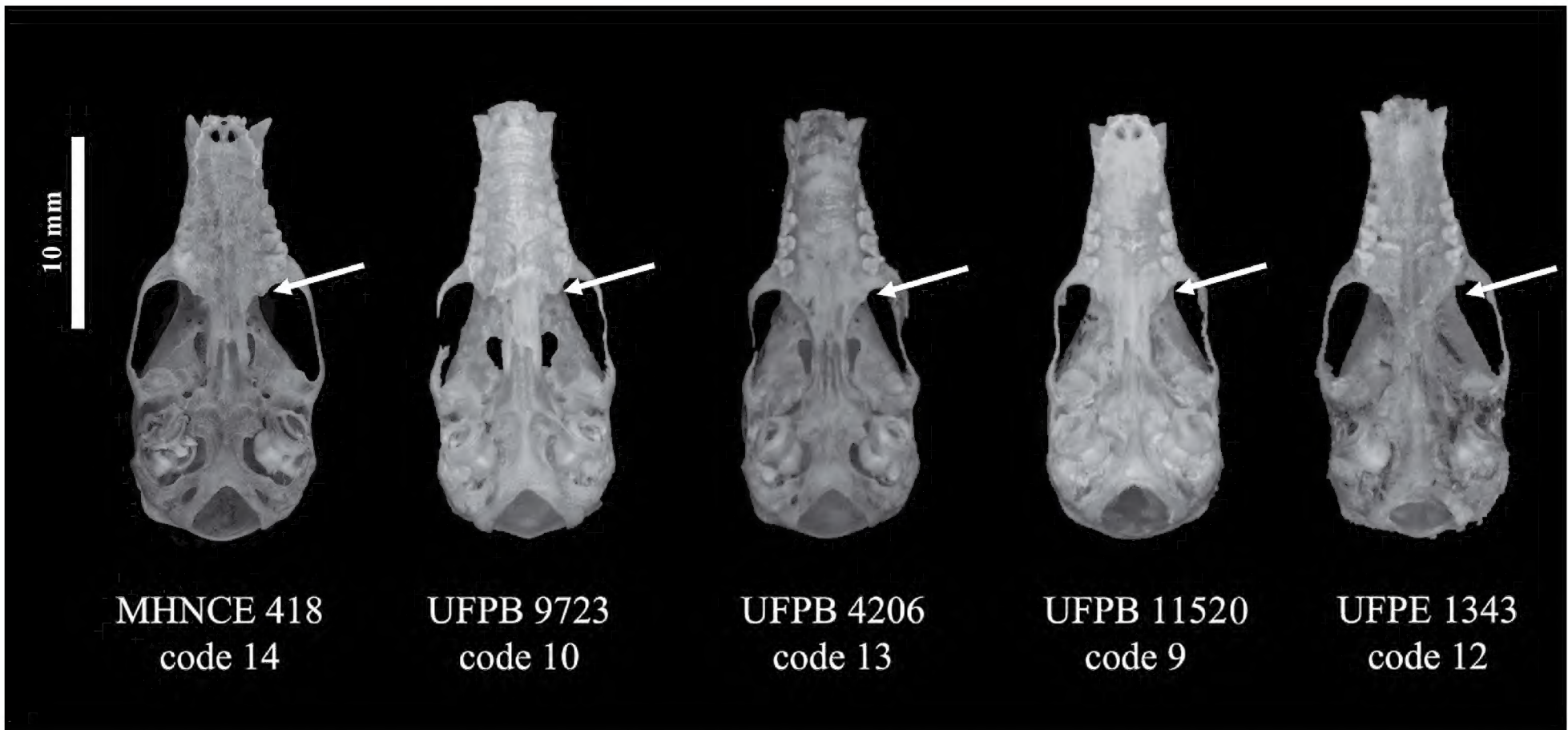


Figure 3. Ventral view of the skulls of individuals of *Anoura caudifer*. Codes represent the location of the specimens in Table 1 and Figure 1. Note the difference in the development of the posterior margin of the palate.

distinct from *A. caudifer* because it lacks a palatal process and has a larger skull ($24.30\text{ mm} \pm 0.48$) (Pacheco et al. 2018). From *A. aequatoris* the distance between C and P2 is larger in *A. caudifer*, and *Anoura aequatoris* has a deeper hypocone basin compared to *A. caudifer* (Mantilla-Meluk and Baker 2010).

Although the specimens of *A. caudifer* from northeastern Brazil are similar overall to descriptions of *A. caudifer* from elsewhere, we recorded some noteworthy variation. The specimen from Ceará (MHNCE 418) had a relatively furred uropatagium (Fig. 2) and a tail completely enclosed in the interfemoral membrane; its dorsal fur was two-banded, with a reddish-white base and an olive-brown tip, and its ventral fur was bicolored, with a dark base and light tip. Also, the distal border of the uropatagium was circular. The posterior margin of the palate was little-developed in the Guaramiranga specimen (MHNCE 418) and in the Mata de Coimbra specimen (UFPE 4206) and absent in the Pedra Talhada specimens (UFPE 1342 and UFPE 1343) (Fig. 3). The tails surpassed the uropatagium in all Bahia specimens and were totally enclosed in the uropatagium in the Guaramiranga (MHNCE 418) and the Ibateguara (UFPB 4206) specimens.

Literature records. The distribution of *A. caudifer* includes French Guiana, Suriname, Guyana, Venezuela, Colombia, Ecuador, Peru, Bolivia, Argentina, and Brazil. In Brazil, there are records from the North Region (Pará), Center-Western Region (Goiás, Mato Grosso do Sul, Mato Grosso, and Distrito Federal), South Region

Table 1. Records of *Anoura caudifer* in northeastern Brazil. States abbreviations: AL = Alagoas, BA = Bahia, CE = Ceará. Code numbers correspond to the localities in Figure 1.

Code	State	Locality	Latitude	Longitude	Biome	Source
1	BA	Canavieiras	−15.670	−038.946	Atlantic Forest	Faria et al. 2006
2	BA	Pau Brasil	−15.465	−039.651	Atlantic Forest	Faria et al. 2006
3	BA	Una	−15.296	−039.075	Atlantic Forest	Faria et al. 2006; Faria and Baumgarten 2007
4	BA	Ilhéus	−14.797	−039.048	Atlantic Forest	Vaz 2005; Faria et al. 2006; Lapenta and Bueno 2015
5	BA	Jequié	−13.851	−040.083	Atlantic Forest	Lapenta and Bueno 2015
6	BA	Palmeiras	−12.520	−041.558	Caatinga	Sbragia and Cardoso 2008
7	BA	São Desidério	−12.485	−045.152	Cerrado	Lapenta and Bueno 2015
8	BA	Morro do Chapéu	−11.554	−041.155	Caatinga	Sbragia and Cardoso 2008
9	BA	Gentio do Ouro	−11.301	−042.656	Caatinga	This study
10	BA	Piçarrão Sento Sé	−09.745	−041.885	Caatinga	This study
11	AL	Traipu	−09.740	−036.951	Caatinga	Silva and Palmeira 2014
12	AL	Quebrangulo	−09.318	−036.470	Atlantic Forest	Guerra 2015
13	AL	Ibateguara	−09.009	−035.892	Atlantic Forest	Sá-Neto 2003
14	CE	Guaramiranga	−04.262	−038.932	Caatinga, Brejo de altitudes	This study

(Rio Grande do Sul, Santa Catarina, and Paraná), and Southeast Region (Rio de Janeiro, São Paulo, Espírito Santo, and Minas Gerais). The literature includes 11 records from the Northeast Region of Brazil (Bahia and Alagoas). Records from Bahia were from the Atlantic Forest (municipalities of Canavieiras, Pau Brasil, Una, Ilhéus and Jequié), the Cerrado (São Desidério), and Caatinga (Palmeiras and Morro do Chapéu). In Alagoas, *A. caudifer* has been recorded from the Atlantic Forest (Quebrangulo and Ibateguara) and Caatinga (Traipu) (Table 1).

DISCUSSION

With our new records, we expand the known geographic distribution of *Anoura caudifer* in northeastern Brazil. The record from Ceará state expands the distribution of *A. caudifer* by over 600 km north of its nearest previously known locality in Brazil. We register the occurrence of *A. caudifer* in the state of Ceará, as predicted by Weber and Grelle (2012), adding one more species to the list of bats known for the state, which now has 48 bat species records (Gurgel-Filho et al. 2015; Novaes and Laurindo 2014; da Silva et al. 2015; Leal and Bernard 2021).

Within Brazil, *A. caudifer* has often been said to be associated with forested and humid areas (Oprea et al. 2009) at elevations from sea level to 1500 m (Eisenberg 1989) in Atlantic Forest, Cerrado, Pantanal, and the Amazon Basin (Griffiths and Gardner 2008; Solari et al. 2020; Marsh et al. 2022; Molinari et al. 2023). In the Amazon biome, this species has been recorded in Amapá (Peracchi et al. 1984; Santos and Gibson 1998; Mourão et al. 2002; Martins et al. 2006; Martins et al. 2011), which is on the Guiana Shield (Tavares et al. 2017; Lim and Lee 2018). The Guiana Shield has probably served as a pathway for expansion of Neotropical bats from the Andes, where the genus appears to have originated (Velazco and Patterson 2008; Camillo-Calderón et al. 2022). In the central Amazonia, *A. caudifer* has been recorded in Manaus, and in eastern Amazonia, from the Floresta Nacional (FLONA) Carajás, Pará (Reis and Peracchi 1987; Tavares et al. 2012). We suggest that the specimens attributed to *A. caudifer* from Amazonia need revision to elucidate the relationships of central and eastern Amazonian populations with Atlantic Forest populations of this species. Knowledge of *Anoura* diversity has greatly expanded in recent years, with half of the *Anoura* species having been described in the last 18 years (Muchhala et al. 2005; Mantilla-Meluk and Baker 2006; Mantilla-Meluk and Baker 2010; Pacheco et al. 2018), but little revisionary work has been conducted with eastern South American forms. Thus, the existence of distinct, unrecognized species is likely.

The Guaramiranga locality is composed of wetlands, at 865 m in elevation, inserted in semiarid lowlands. These unique ecosystems, known as “Brejos de altitude” (altitude swamps) are immersed in the semiarid Caatinga biome and are characterized by the occurrence of highland moist areas interspersed within xeric landscapes, creating “islands” of humidity in regions with a high concentration of rainfall (Moro et al. 2015). Likewise, all our new records and literature records listed herein are from ecosystems moister than the Caatinga itself. Traipu, in Alagoas state, is part of the Serra das Mãos, a mosaic of Atlantic Forest and Caatinga associated ecosystems (Oliveira et al. 2014). Palmeiras, Morro do Chapéu and Gentio do Ouro, and Chapada Diamantina in Bahia are well-drained plateau composed of a mosaic of Caatinga, Cerrado, and forest (Juncá et al. 2005; Lobão et al. 2011; França et al. 2013; Santos et al. 2023). Piçarrão, which lies in the valleys of perennial rivers of the Depressão Sertaneja Meridional, is densely forested (Rocha et al. 2015).

Although *A. caudifer* is a not uncommon and has a wide distribution in South America, basic information and knowledge regarding morphology variation are largely lacking, and its differentiation from similar species is often unclear. There is recurrent disagreement, for example, in the use of size to separate *A. caudifer* from its sister species, and maximum skull sizes vary in the literature (e.g. Molinari 1994; Dias et al. 2002; Griffiths and Gardner 2008; Pacheco et al. 2018). The tail of *A. caudifer* is also variable in length and can be either totally enclosed in the interfemoral membrane or surpass it. On the other hand, most specimens collected in Brazil and examined up to the early years 2000 had longer tails surpassing the uropatagium (Dias et al. 2002; Table 2). Some authors (see Oprea et al. 2009) suggested that there is little morphological variation in *A. caudifer*. In contrast, we observed in a single sample of specimens from northeastern Brazil considerable, previously unreported variation in the presence and density of fur in the uropatagium, and in the shape and extension of the distal margin of the palatal processes. The uropatagium of *A. caudifer* is often little-haired (Dobson 1878; Allen 1898; Sanborn 1933; Husson 1962; Tamsitt and Valdivieso 1966; Oprea et al. 2009), but we observed a gradation of few-haired to more-haired uropatagia in Brazilian specimens, such as the Ceará specimen; similar variation occurs in other species of the *A. caudifer* complex (Molinari 1994; Mantilla-Meluk and Baker 2006; Pacheco et al. 2018). The variation in the shape of the posterior border of the palate of *A. caudifer* was also observed by Pacheco et al. (2018).

Our data reinforce the probability that the distribution of *A. caudifer* is connected to forested, moister habitats, which includes forest patches interspersed in dry landscapes. Therefore, we suggest that efforts to sample additional humid, forested sites will probably find additional records and refine the knowledge of the distribution of *A. caudifer*. We observed undescribed morphological variation of this species that suggest a need for revisionary work and increased collection effort.

Table 2. External and cranial measurements and body mass of *Anoura caudifer* reported here. All linear measurements are in millimeters (mm) and weights in grams (g).

	Ceará			Alagoas		Bahia	
	Guaramiranda	Ibateguara	Quebrangulo	Gentio do Ouro	Gentio do Ouro	Piçarrão	Piçarrão
	MHNCE 418	UFPB 4206	UFPE 1342, 1343	UFPB 11520, 11521	UFPB 11523	UFPB 6491, 6492, 6643, 6668, 9723, 11500	UFPB 6651, 11496
Sex	Male	Male	Male	Female	Male	Female	Male
Weight	12.5						
FA	35.61	37.38	35.70 ± 0.30 (35.4–36)	35.47 ± 1.33 (34.14–36.80)	37.58	36.46 ± 0.59 (35.68–37.30)	36. 27 ± 0.41 (35.85–36.68)
Tail	Enclosed in uropatagium	Enclosed in uropatagium	—	Surpasses uropatagium	Surpasses uropatagium	Surpasses uropatagium	Surpasses uropatagium
GLS	22.59	22.74	23.04 ± 0.1 (23.03–23.05)	21.83 ± 0.4 (21.42– 22.23)	22.21	22.86 ± 0.28 (22.38–23.22)	22.74 ± 0.18 (22.56–22.91)
PAL	12.63	13.02	13.7 ± 0.14 (13.56–13.83)	12.65 ± 0.55 (12.10–13.19)	13.75	10.96 ± 0.53 (12.28–13.72)	12.84 ± 0.16 (12.68–12.99)
MTRL	8.37	8.34	8.36 ± 0.01 (8.35–8.37)	7.9 ± 0.24 (7.66–8.14)	8.14	8.37 ± 0.2 (8.05–8.62)	8.05 ± 0.1 (7.95–8.14)
M3-M3	3.57	3.35	3.39 ± 0.05 (3.34–3.44)	3.13 ± 0.01 (3.12–3.14)	3.18	3.22 ± 0.15 (2.96–3.45)	3.12 ± 0.02 (3.10–3.14)
C-C	4.30	4.07	4.35 ± 0.09 (4.26–4.43)	3.78 ± 0.02 (3.76–3.79)	3.88	3.91 ± 0.11 (3.67–4.01)	3.94 ± 0.01 (3.93–3.95)
CBL	21.73	21.40	21.61 ± 0.09 (21.52–21.69)	20.31 ± 0.41 (19.9–20.72)	20.79	21.39 ± 0.17 (21.08–21.59)	21.28 ± 0.08 (21.2–21.36)
HBC	7.60	7.08	7.47 ± 0.06 (7.40–7.53)	7.49 ± 0.17 (7.32–7.66)	7.94	7.44 ± 0.26 (7.09–7.77)	6.74 ± 0.21 (6.53–6.95)
PB	4.61	4.51	4.5 ± 0.05 (4.45–4.55)	4.29 ± 0.06 (4.23–4.35)	4.76	4.65 ± 0.07 (4.54–4.72)	4.58 ± 0.23 (4.35–4.8)
MB	9.12	8.69	8.99 ± 0.04 (8.94–9.03)	8.25 ± 0.03 (.21–8.28)	9.26	8.6 ± 0.09 (8.46–8.72)	8.87 ± 0.12 (8.75–8.98)
BCB	9.11	8.85	8.93 ± 0.09 (8.84–9.01)	8.53 ± 0.05 (8.48–8.58)	9.18	8.99 ± 0.18 (8.74–9.24)	8.66 ± 0.08 (8.58–8.74)
MANL	16.32	16.57	16.45 ± 0.32 (16.13–16.76)	15.55 ± 0.49 (15.06–16.03)	16.30	16.21 ± 0.32 (15.79–16.74)	15.92 ± 0.21 (15.71–16.13)
MANTRL	9.23	8.89	8.82 ± 0 (8.82–8.82)	8.22 ± 0.23 (7.98–8.45)	8.76	8.61 ± 0.24 (8.39–9.08)	8.48 ± 0.2 (8.28–8.68)

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ADDITIONAL INFORMATION

Conflict of interest

The authors declare that no competing interests exist.

Ethical statement

No ethical statement is reported.

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Author contributions


Conceptualization: BDN, MBO, PAR, VCT. Data curation: BDN, VCT. Investigation: BDN, MBO, PAR, NMCSC, JLPC, VCT. Methodology: BDN, MBO, PAR, VCT. Resources: BDN, VCT. Supervision: VCT. Visualization: BDN,

MBO, PAR, NMCSC, JLPC, VCT. Writing – original draft: BDN, VCT. Writing – review and editing: BDN, MBO, PAR, NMCSC, JLPC, VCT.


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Data availability

All data that support the findings of this study are available in the main text.

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